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Geographic Variation in Cranial Morphology of the Southern Mountain Cavy, *Microcavia australis* (Rodentia, Caviidae): Taxonomic Implications, with the Description of a New Species

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Pablo Teta, Ricardo A. Ojeda, Sergio O. Lucero, and Guillermo D'Elía (2017) We analyzed the geographic variation in cranial morphology of the Southern Mountain Cavy, *Microcavia australis*, throughout of its distributional range. Our analysis allows us to recognize three geographically allopatric morphotypes. These morphotypes differ in the general size and shape of the skull and discrete morphological traits of the zygomatic arch, palate and mesopterygoid fossa. Based on these results, we restrict the name *australis* to populations distributed in southern Argentina and west-central Andes and the name *maenas* to the morphotype of northwestern and central Argentina. The third morphotype occurs in the Dry Chaco ecoregion and is described here as a new species.

Key words: Caviomorpha, Cavioidea, Cranial variation, Qualitative morphology, Quantitative morphology.

BACKGROUND

The genus *Microcavia* H. Gervais and Ameghino, 1880 includes three living and at least four fossil species of small (< 400 g), semifossorial and herbivorous caviomorph rodents endemic to southern South America (Quintana 1996; Ubilla et al. 1999; Dunnum 2015). Among the living forms, *M. niata* (Thomas, 1898) and *M. shiptoni* (Thomas, 1925) are restricted to highland areas of northwestern Argentina, southwestern Bolivia and northern Chile, while *M. australis* (I. Geoffroy and d'Orbigny, 1833) ranges widely from northwestern Argentina to southern Argentinean and Chilean Patagonia (Rood 1970; Tognelli et al. 2001).

As for other caviids (*e.g.*, *Cavia*, *Galea*), our knowledge about the level and patterns of inter- and intraspecific morphological variation of *Microcavia* is limited, resulting in varied taxonomic conclusions (*e.g.*, Dunnum 2015). For instance, Thomas (1921) recognized five subspecies of *M. australis*, from north to south: *maenas* Thomas, 1898, *salinia* Thomas, 1921, *joannia* Thomas, 1921, *nigriana* Thomas, 1921, and *australis* (including *kingii* Bennett, 1836 in its synonymy). This taxonomic arrangement was followed with some modifications by Ellerman (1940), who distinguished *kingii* at the subspecies level and included *nigriana* into the synonymy of *australis*. Later, Cabrera (1953) hypothesized a simpler scenario, recognizing only three subspecies within *australis*: *maenas*, *salinia* and *australis* (including *joannia*, *kingii* and *nigriana* as synonyms). Thomas (1921) and Cabrera (1953) each based their taxonomic hypotheses on cranial traits and differences in external coloration of small series of individuals.

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Dunnum (2015), in the most recent treatment of the genus, follows the scheme of Cabrera (1953) and recognized, mostly based on morphological data (see also Tognelli et al. 2001), three subspecies of *M. australis*. Sassi et al. (2011b), using molecular markers, found high levels of divergence among highland and lowland cavy populations of west-central Argentina, a scenario that suggests that this taxon may encompass more than one form. According to these authors, mean sequence divergence in a fragment of the mitochrondrial genome among populations from different altitudes was around 9%. In agreement with these results, Taraborelli et al. (2007) detected some variation in cranial size along an altitudinal gradient in the same general area.

The main purpose of our study is to test prior taxonomic hypotheses by means of cranial and skin morphology analyses among populations currently assigned to *M. australis*. The study is based on a large sample of specimens, by far the largest yet analyzed, both in terms of specimen number and geographic coverage; it includes holotypes or topotypes of all nominal forms.

MATERIALS AND METHODS

Specimens examined

We examined 272 subadults and adults assigned to *Microcavia australis.* Specimens document 66 localities (Fig. 1) and include the holotypes of the nominal forms *joannia*, *maenas*, *nigriana*, and *salinia*. Specimens examined are housed in the following museums and collections: The Natural History Museum (BM, London, UK); Colección Elio Massoia (CEM, acquired by the Fundación de Histora Natural Félix de Azara, Buenos Aires, Argentina); Colección de Mamíferos

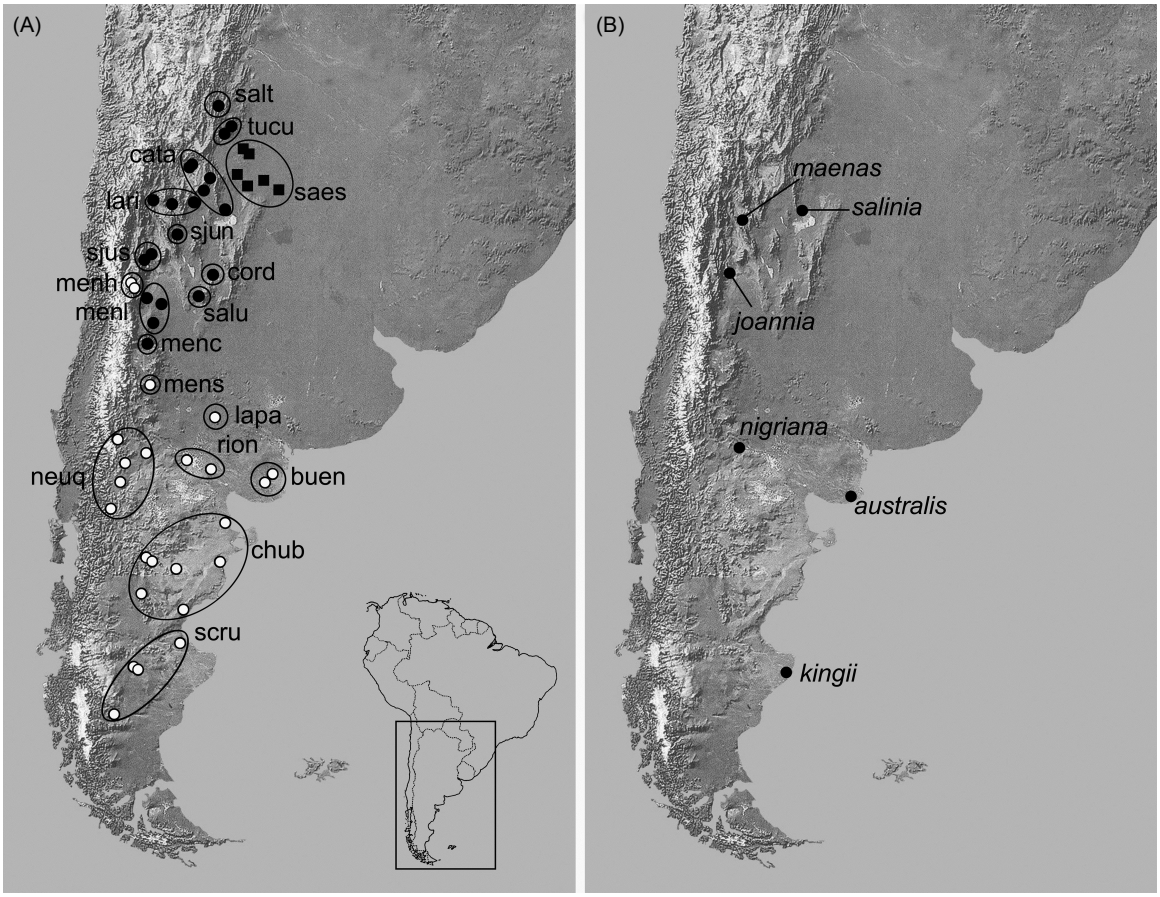

Fig. 1. A: map of southern South America indicating the collecting localities of the examined specimens of *Microcavia*. Ellipses shown the groupings of localities that constitute the geographical samples analyzed. See Materials and Methods for an explanation of the acronyms. Different symbols correspond to the three species identified in this work: white circles = *M. australis*; black circles = *M. maenas*; black squares = *M. jayat* n. sp. B. map of southern South America indicating the type localities of names associated with *Microcavia australis*.

del Instituto Argentino de Investigación de Zonas Áridas (CMI, Mendoza, Argentina); Colección de Mamíferos de la Facultad de Ciencias Naturales e Instituto Miguel Lillo (CML, Tucumán, Argentina); Colección de Mamíferos del Centro Nacional Patagónico (CNP, Chubut, Argentina); and Colección Nacional de Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN, Buenos Aires, Argentina. Analyzed specimens and their localities are listed in the Supplementary 1.

Cranial measurements

Sixteen craniodental measurements were recorded from each specimen by one of the authors (P. Teta) using a digital caliper to the nearest 0.01 mm: total length of the skull (TLS); condylo-incisive length (CIL); interorbital constriction (IOC); greatest zygomatic breadth (ZB); breadth of braincase (BB); length of nasals (NL); width of nasals (NW); length of frontals (FL); length of the upper diastema (DL); length of incisive foramina (LIF); breadth of incisive foramina (BIF); length of upper toothrow (TRL); palatal length (PL); breadth of palate at the level of the upper third molar (BPM3); breadth across the paraoccipital processes (BPP); and length of tympanic bullae (TBL). The definition of these measurements follows Contreras and Contreras (1984) and Ubilla and Rinderknecht (2014), with modifications (see Fig. 2).

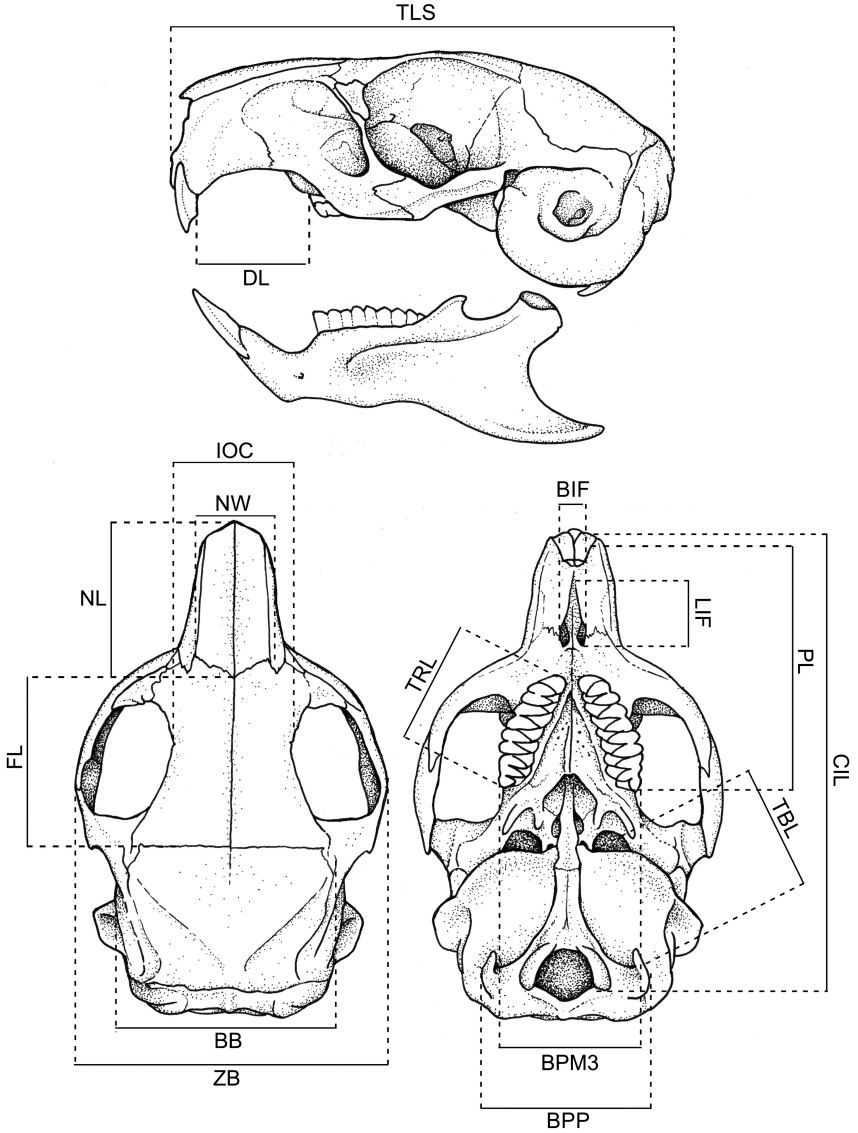

Fig. 2. Skull of *Microcavia* indicating the measurements used in this study. Refer to the text for measurement acronyms.

Geographic variation

Geographic samples (Fig. 1) were established according to the specimens available; a few samples were represented by a single locality but many others were obtained by pooling specimens from nearby localities (*e.g.*, Musser 1968). This action was needed to obtain larger sample sizes amenable for statistical analyses. We used geographic proximity, absence of major geographical barriers among localities, and lack of obvious discrepancy in size and shape among specimens (see examples of this approach in Brennand et al. 2013; Chiquito et al. 2014; Libardi and Percequillo 2016) to construct the samples. The following groups were constituted: buen, southern Buenos Aires Province (*N* = 1); cata, Catamarca Province (*N* = 9); chub, Chubut Province (*N* = 19); cord, western Córdoba Province (*N* = 4); lapa, La Pampa Province (*N* = 1); lari, La Rioja Province (*N* = 40); menc, central Mendoza Province (*N* = 1); menh, northwestern highland Mendoza Province (*N* = 1); menl, northern lowland Mendoza Province (*N* = 20); mens, southern Mendoza Province (*N* = 2); neuq, Neuquén Province (*N* = 8); rion, Río Negro Province (*N* = 5); saes, Santiago del Estero Province (*N* = 8); salt: southwestern Salta Province (*N* = 5); salu, northern San Luis Province (*N* = 3); scru, Santa Cruz Province (*N* = 5); sjun, northeastern San Juan Province (*N* = 4); sjus, southern San Juan Province (*N* = 11); and tucu, Tucumán Province (*N* = 2). Anatomical terminology for cranial and dental features follows Cherem and Ferigolo (2012), with modifications. Analyses of qualitative characters of the skull and dentition were conducted using Thomas (1921), Kraglievich (1930) and Cabrera (1953) as data sources.

Statistical analyses

Patterns of geographic variation were assessed through descriptive statistics (i.e., mean, minimum and maximum values, standard deviation) and multivariate analyses, including principal component and discriminant function analyses (PCA and DFA, respectively). PCA was performed on a subsample of 144 adults (age classes 3-5; following Bezerra 2008), using log10-transformed data to normalize the contribution of each measurement to the total variance. Principal components (PCs) were extracted from the variance-covariance matrix (Strauss 2010). Discriminant function analyses (DFA) were employed to assess the variable contributing to differentiate between samples (Strauss 2010). Finally, we also calculated the squared Mahalanobis (D^2) distances among geographical samples with more than 5 individuals, depicting them in a dendrogram based on the unweighted pair-group method by using arithmetic averages (UPGMA; Sneath and Sokal 1973). All statistical *analyses were* carried out with *InfoStat software* (Di Rienzo et al. 2008).

RESULTS

Qualitative morphological variation

Studied specimens have a relatively broad, bowed and short skull, that has its highest part over the posterior zygomatic root; rounded orbits; large incisive foramina, nearly triangular in outline, and large bullae (Figs. 3 and 4). Samples are also remarkably uniform in external appearance; no differences are noted in the distribution of vibrissae, or any gross aspect of the ears or feet, including the number of plantar pads. Most specimens exhibit a brownish to olive or grayish

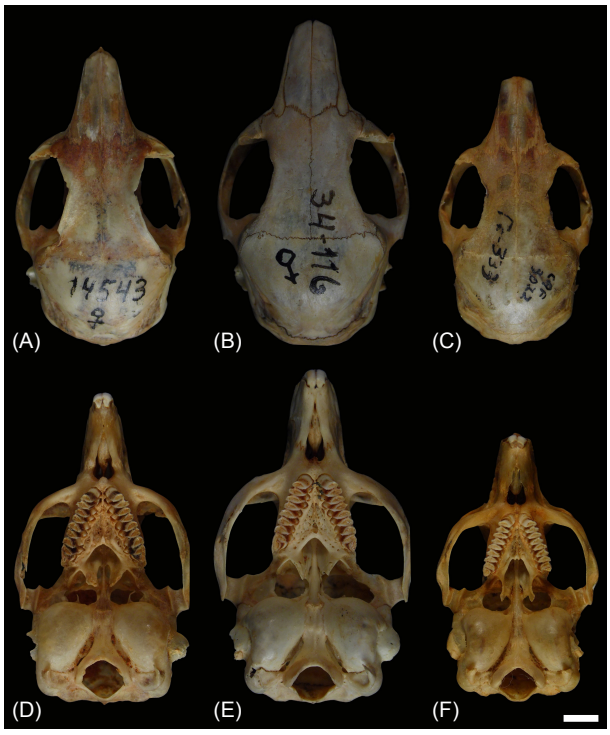

Fig. 3. Dorsal (A-C) and ventral (D-F) views of the skull of three species of *Microcavia*: *M. australis* (A, D; MACN-Ma 14.543), *M. maenas* (B, E; MACN-Ma 34.116) and *Microcavia* n. sp. (C, F; MACN-Ma 17333). Scale bars = 5 mm.

dorsal coloration, with a more or less marked agouti effect; underparts are grayish to yellowish, usually with a patch of dark gray hairs on the neck. However, as detailed below, specimens vary in overall saturation of pigments as well as some differences in qualitative and quantitative cranial traits (see Supplementary 2).

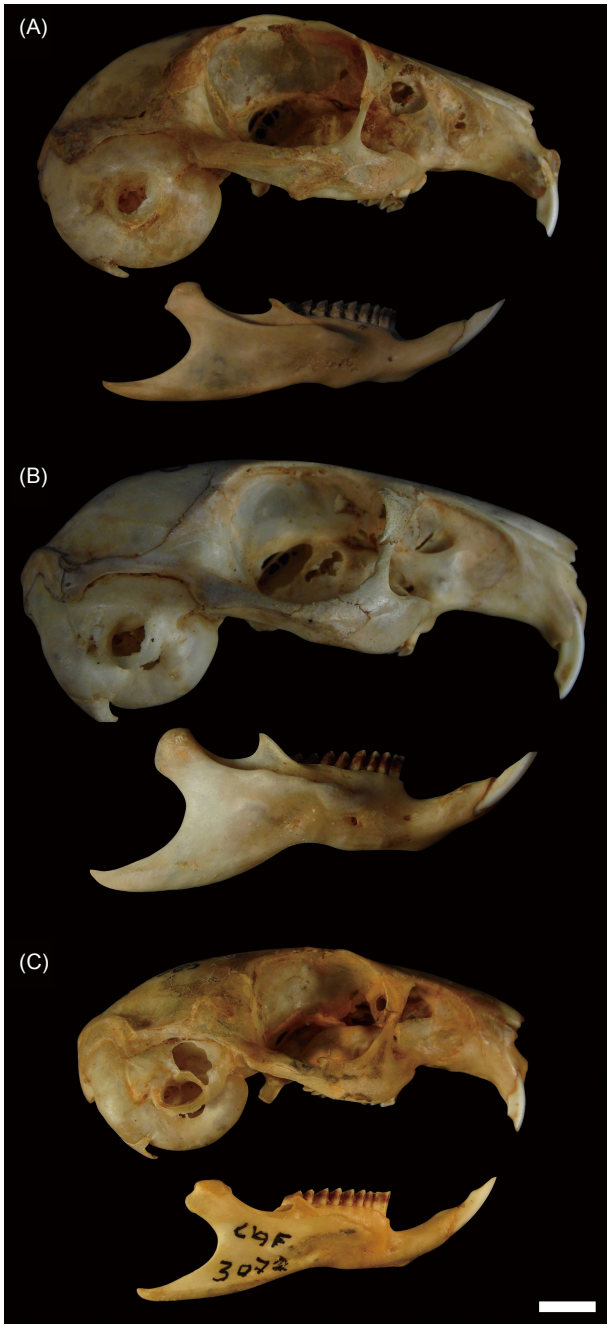

Fig. 4. Lateral views of the skull and right dentaries in labial views of three species of *Microcavia*: *M. australis* (A; MACN-Ma 14.543), *M. maenas* (B; MACN-Ma 34.116) and *Microcavia* n. sp. (C; MACN-Ma 17331). Scale bars = 5 mm.

Three main morphotypes within the current concept of *Microcavia australis* were recognized on the base of discrete and constant differences in the zygomatic arch, palate, and mesopterygoid fossa (Figs. 5 and 6), as well as in size and shape of the skull (see the section below). Most of these characters, such as the presence of a paraorbitary process, the form of the anterior border of the mesopterygoid fossa, and the size and shape of the sphenopalatine vacuities, do not vary within morphotypes and as such their variation is geographically structured. These differences are evident in most of the specimens, even when more than half of the studied crania have the post palatal portion broken.

Morphotype 1 includes buen, chub, lapa, menh, mens, neuq, rion and scru samples, which have bowed to strongly bowed parietals; inferior process of the jugal extended to the level of the posterior border of the glenoid fossa (Fig. 5A); suture between palatines occupied by a triangular to more or less heart-shaped palatal crista; rounded to acute posterior palatal edges, large sphenopalatine vacuities and relatively narrow presphenoids (Figs. 5B and 6). Externally, this morphotype includes specimens with brownish to olive dorsal coloration, in a well-marked agouti pattern, and grayish to yellowish venter. Representatives of populations currently assigned to the subspecies *M. a. australis*, including topotypes of *nigriana* and *australis*, exhibit this morphotype.

In turn, morphotype 2 is represented by specimens from cata, cord, lari, menc, menl, sjun, sjus, salt, salu, and tucu, which have a more flattened dorsal profile of the skull; inferior process of the jugal posteriorly extended beyond the border of the glenoid fossa (Fig. 7); long and narrow to long and slightly rhomboidal palatal crista along the suture between palatine bones; usually angled to rounded posterior palatal edges, sometimes with a distinctive nasal spine; proportionally smaller sphenopalatine vacuities, and broad presphenoids (Figs. 5-6). The dorsal coloration of this morphotype is more yellowish to grayish, with less evident agouti pattern. Specimens currently referred to *maenas* and *salinia*, including the holotypes of *joannia*, *maenas*, and *salinia* exhibit the diagnostic attributes of morphotype 2.

Finally, morphotype 3 is only present in the sample referred as saes, which has an unique combination of character states, including a relatively flattened dorsal profile to the skull; inferior process of the jugal posteriorly extended beyond

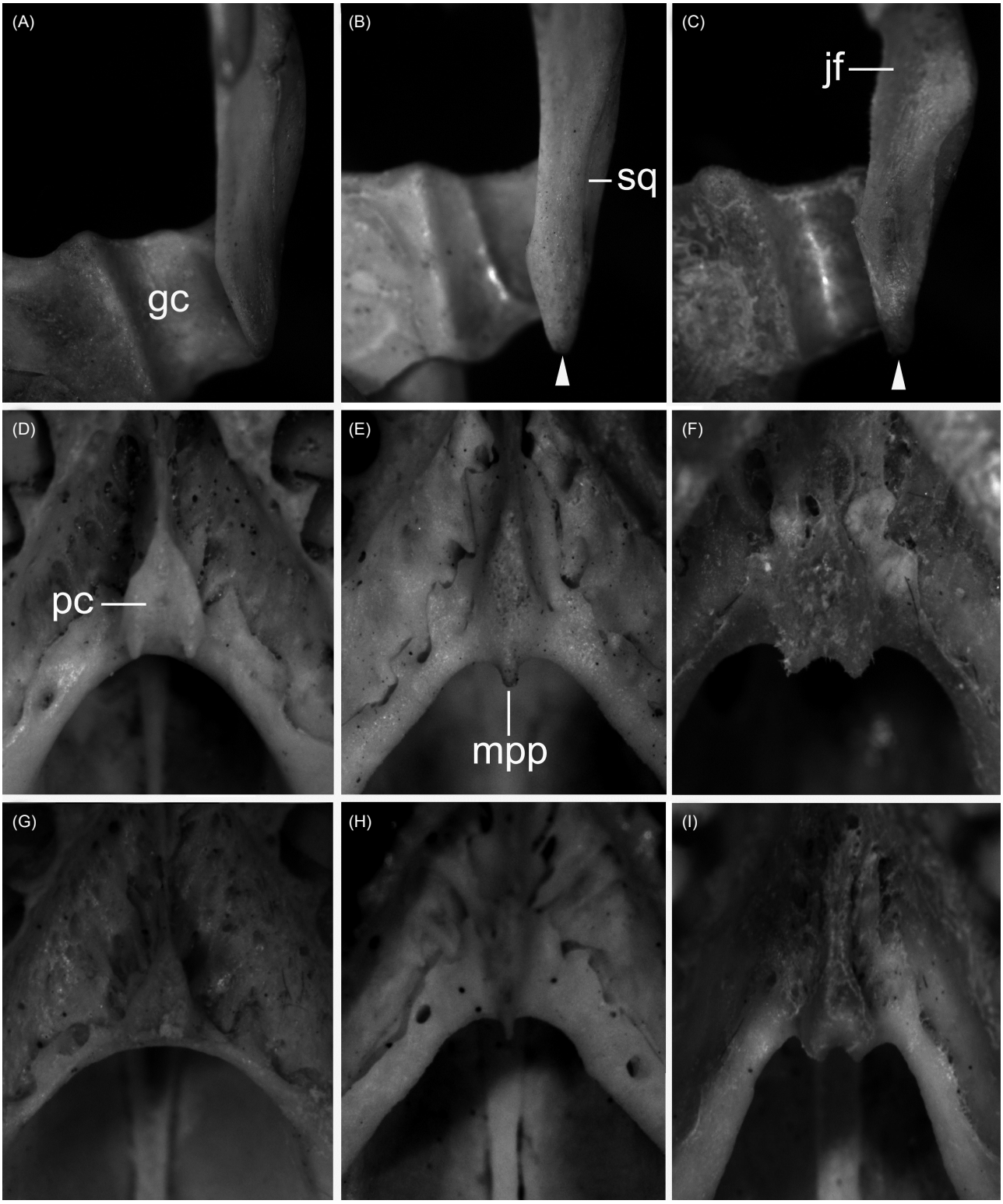

Fig. 5. Selected anatomical traits of three species of *Microcavia* (A, MACN-Ma 16379; B, MACN-Ma 34.81; C, MACN-Ma 17331; D, MACN-Ma 16379; E, MACN-Ma 36.72; F, MACN-Ma 17333; G, MACN-Ma 28.51; H, MACN-Ma 36.84; I, MACN-Ma 17331), depicting the relative position of inferior process of the jugal (marked by the arrow) relative to the glenoid cavity (a-c) and size and shape of the palatal cristae (d-i). A, D, G = *M. australis*; B, E, H = *M. maenas*; C, F, I = *M*. n. sp. Abbreviations: gc = glenoid cavity; jf = jugal fossa; mpp = medial process of the palate; pc = palatal crista; sq = squamosal. Photographs are not in scale to facilitate comparisons among proportions.

the border of the glenoid fossa (Fig. 5C); suture between palatines occupied by a heart-shaped palatal crista that surpasses the posterior border of the palate, which has a nearly trapezoidal outline; small sphenopalatine vacuities and relatively broad presphenoids (Figs. 5 and 6). An additional unique feature of these specimens is the presence of a small but conspicuous paraorbital process on the zygomatic arch formed exclusively by the jugal (Fig. 7). Pelage coloration of morphotype 3 is yellowish brown, with grayish underparts; some individuals have conspicuous patches of pure white hairs at the throat, the inner side of the fore and hindfeet, and in the inguinal region. No name is available for this morphotype.

Quantitative morphological variation

PCA revealed that all variables were positively correlated with the 1st principal component (PC1 57%), indicating that it summarizes mainly latent size variation (see Tables 1 and 2). The plot of individual scores labeled by geographic provenance shows marked overlap of individuals from different samples in relation to the PC1 (Fig. 8A; Table 1). However, when only centroids are considered, two main groups can be recognized, one encompassing buen, chub, lapa, menh, mens, neuq, rion, saes and scru, and a second including cata, cord, lari, menc, menl, sjun, sjus, salu, and tucu. The distribution along the 2nd principal

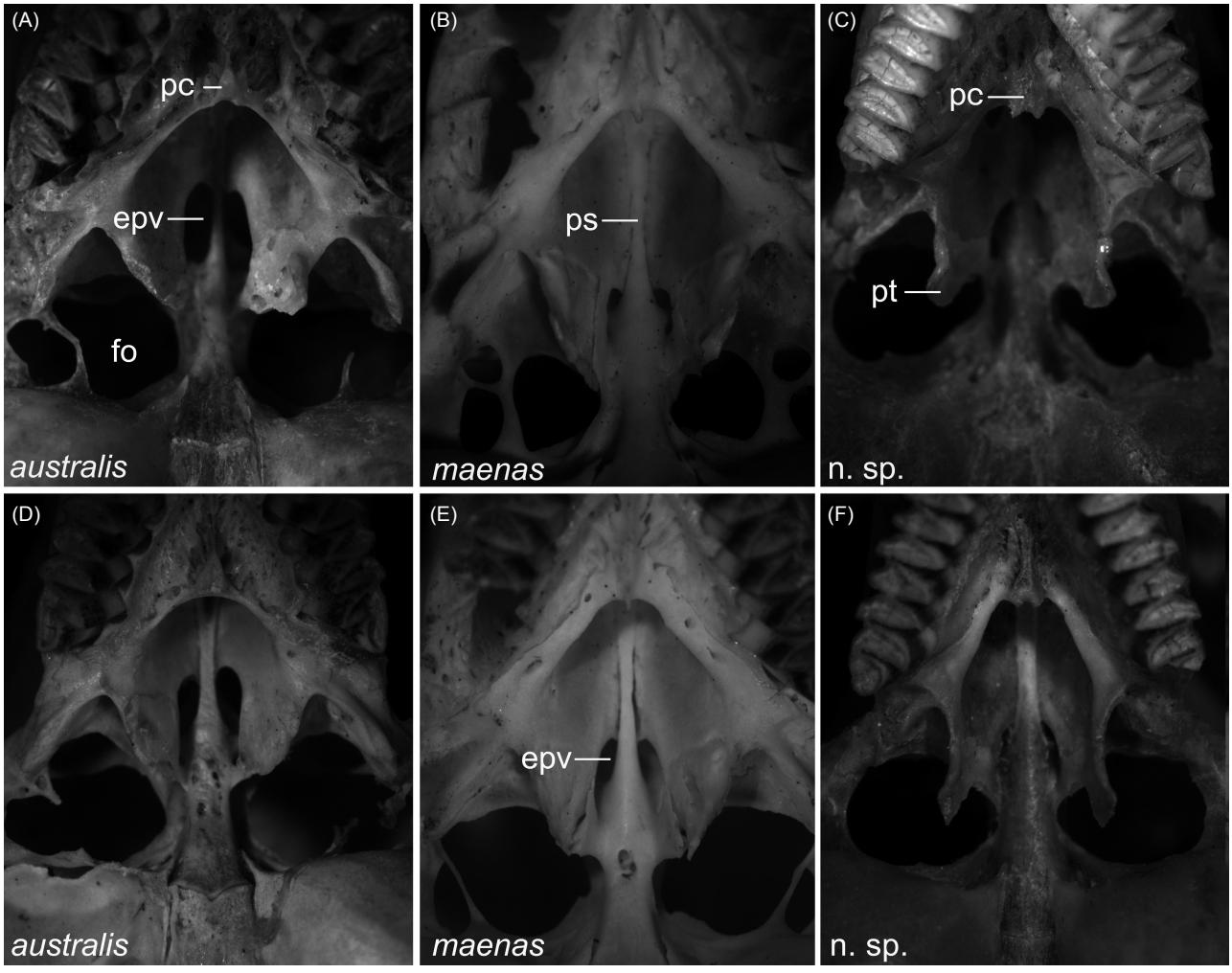

Fig. 6. Selected anatomical traits of three species of *Microcavia* (A, MACN-Ma 14543; B, MACN-Ma 36.72; C, MACN-Ma 17331; D, MACN-Ma 25.51; E, MACN-Ma 36.84; F MACN-Ma 17333), depicting the contour of the posterior border of the palate and size of sphenopalatine vacuities (epv). Abbreviations: fo = foramen oval; pc = palatal crista; ps = presphenoid; pt = pterygoid. Photographs are not in scale to facilitate comparisons among proportions.

component (PC2 7%, Fig. 8A) does not reveal any clear pattern, with broad overlap among pooled samples.
Table 2.

The DFA revealed three major morphometric clusters dispersed along the 1st and 2nd discriminant axes (Fig. 8B; Table 1), which summarize 64% of the variance. The 1st group is composed of samples from buen, chub, lapa, menh, mens, neuq, rion and scru (= morphotype 1), including most of the populations allocated to *M. a. australis*. The 2nd cluster comprises the samples cata, cord, lari, menc, menl, sjun, sjus, salu, and tucu (= morphotype 2), compassing those populations referred in the literature as *M. a. maenas* and some of those now identified as *M. a. salinia*. This cluster includes topotypes of *joannia*, *maenas* and *salinia*. Finally, the 3rd cluster is formed by specimens from saes (= morphotype 3), which departs from the other two clusters in both discriminant functions. The classification matrix determined by the discriminant function is presented in the Supplementary 3.

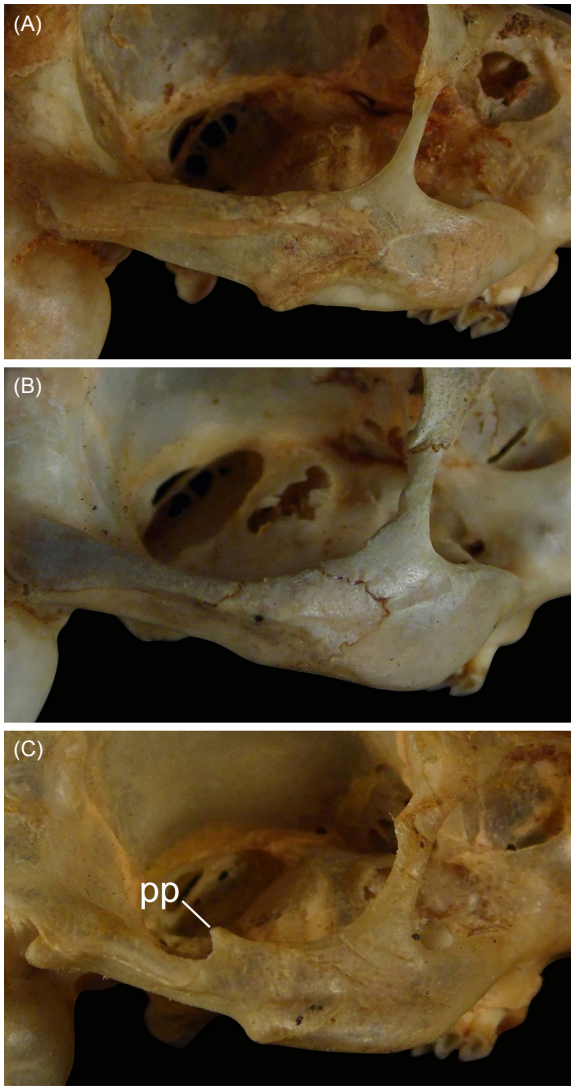

Fig. 7. Lateral view of the zygomatic arch in three species of *Microcavia*: *M. australis* (A; MACN-Ma 14.543), *M. maenas* (B; MACN-Ma 34.116) and *Microcavia* n. sp. (C; MACN-Ma 17333). Abbreviation: pp = paraorbitary process. Photographs are not in scale to facilitate comparisons among proportions.

The holotypes of *joannia*, *maenas*, *nigriana*, and *salinia* (see Table 3) were measured by R. Ojeda, so we opted to exclude these specimens from the multivariate analyses. However, a posteriori classification of the holotypes of *joannia* and *salinia* nested their scores within the cluster of specimen scores represented by the morphotype 2 in the canonical variate plots, while the holotype of *nigriana* grouped with those samples referred to morphotype 1 (results not shown).

The UPGMA supports the geographic clustering into three main groups; one composed by samples referred to morphotype 1 from chub, menh, neuq, rion and scru; another corresponds to morphotype 2 comprised of samples from cata, lari, menl, and sjus. The sample from saes, the sole representative of morphotype 3, remained as a divergent unit, eventually joined to morphotype 1 group (Fig. 9).

Based on the results of qualitative and quantitative analyses of cranial traits, we conducted a between-group PCA and an additional DFA pooling the samples into three main morphotypes (labeled here as *australis* [= morphotype 1], *maenas* [= morphotype 2], and n. sp. [= morphotype 3]). Results of these analyses are shown in figures 8C and 8D (tables not shown), which strongly support the recognition of three morphological entities among populations referred to *M. australis*.

Craniodental measurements, including mean, standard deviation (*SD*), and range, are summarized in table 2; external measurements are provided in the Supplementary 4. Abbreviations: M1/m1, first upper/lower molar; M2/m2, second upper/lower molar; M3/m3, third upper/lower molar; PM4/pm4, fourth upper/lower premolar.

Taxonomy

The results of quantitative and qualitative morphological analyses support the existence of three different morphotypes within populations currently referred to *Microcavia australis*.

Qualitative cranial traits are remarkably constant within groups, distinguished them and implying that they independently evolved from each other. As such, the three morphotypes are here regarded as distinct lineages at the species level. We therefore propose that *M. australis* is in fact a species complex, including *M. australis* s.s., *M. maenas* and a third, unnamed species, which is described at the end of this section:

***Microcavia australis* (I. Geoffroy and d'Orbigny, 1833)**

(Figs. 3-6)

C[*avia*]. *australis* I. Geoffroy and d'Orbigny, 1833:1.

Kerodon Kingii Bennett, 1836:190 [type locality "apud Portum Desire dictum, ad Patagoniæ littus orientale" (= Puerto Deseado, Santa Cruz, Argentina)].

Caviella australis nigriana Thomas, 1921:446 [type locality "Neuquen, R. Negro" (= Neuquén, Argentina).

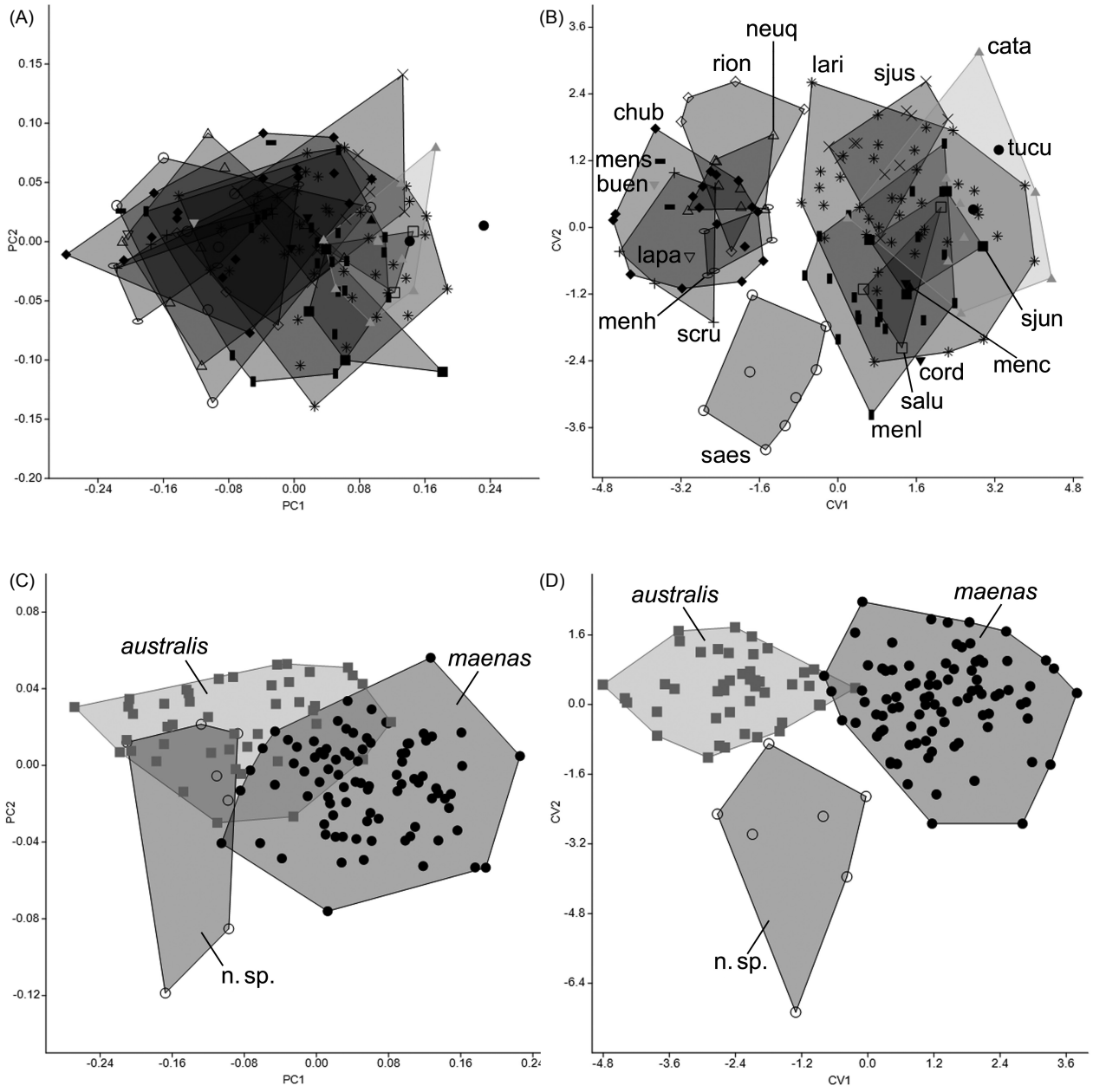

Fig. 8. Specimen scores of adult individuals (ages 3-5) of Microcavia (N = 144) for: A) Principal components 1 and 2; B) Canonical variates 1 and 2, extracted from discriminant function analyses of 18 geographic groups; C) Between morphogroup principal components 1 and 2; D) Canonical variates 1 and 2, extracted from three-group discriminant function analysis. For the acronyms of the geographical samples see Materials and Methods section.

Type locality: "sur les bords du Rio Negro, vers le Quarante- unième degré," restricted to "on the Lower Rio Negro," Río Negro, Argentina (Thomas 1929:44).

Emended morphological diagnosis: A medium-size species of *Microcavia* (length of head and body ca. 188 mm, condylo-incisive length ca. 40 mm) characterized by the following combinations of characters: dorsal coloration brownish to olive brown, with gray to yellowish gray underparts; skull strongly built, wide and relatively short; dorsal profile bowed to strongly

Table 1. Results of principal components analyses (first and second columns) and discriminant function analysis (third and fourth columns) performed on 18 geographic groups of adult specimens of *Microcavia* (*N* = 144). See Materials and Methods for explanation of variable abbreviations

	PC1	PC2	CV1	CV2
TLS	0.32	-0.01	-1.37	2.99
CIL	0.32	-0.04	2.28	-2.53
IOC	0.24	-0.19	0.14	-0.07
ZB	0.28	-0.06	-0.20	-0.14
BB	0.25	-0.16	0.10	0.32
NL	0.29	-0.13	0.93	0.39
NW	0.21	-0.24	0.09	0.16
FL	0.24	0.21	0.34	-0.07
DL	0.29	-0.09	-0.55	-1.30
LIF	0.21	0.14	0.66	0.00
BIF	0.10	0.76	-0.36	0.17
TRL	0.28	-0.07	-0.30	-0.39
PL	0.22	0.05	-0.23	0.28
BPM3	0.25	-0.05	-0.73	0.80
BPP	0.25	0.09	0.15	-0.40
TBL	0.16	0.44	-0.40	0.39
Eigenvalue	9.19	1.14	4.23	1.13
% Variance	57.0	7.0	50.24	13.44

Table 2. Summary statistics (mean, *SD*, range) of cranial measurements (in mm) of adult samples (n) of *Microcavia australis*, *M. maenas* and *M. jayat* n. sp. See Materials and Methods for explanation of the abbreviations

	Microcavia australis					*Microcavia maenas*					*Microcavia jayat* n. sp.				
	n	Mean	*SD*	Min.	Max.	n	Mean	*SD*	Min.	Max.	n	Mean	*SD*	Min.	Max.
TLS	44	45.04	2.44	40.20	49.90	95	48,53	2,10	44,24	54,20	8	44.27	1.15	41.56	45.22
CIL	44	40.26	2.35	35.32	44.50	96	44,06	2,19	39,14	50,00	8	39.99	1.24	37.41	41.42
IOC	44	9.94	0.67	8.77	11.51	99	11,02	0,74	9,48	12,96	8	10.12	0.83	8.85	11.15
ZB	44	27.14	1.25	24.82	29.97	96	28,65	1,56	21,93	32,00	8	26.93	1.61	24.73	30.30
BB	44	21.00	0.68	19.83	22.33	97	21,93	0,85	20,11	23,80	8	20.76	0.96	19.30	22.52
NL	44	14.67	1.01	12.18	16.61	99	16,98	1,11	14,21	19,73	8	14.88	1.23	13.47	17.04
NW	44	6.86	0.56	5.93	8.33	96	7,43	0,56	6,38	9,16	8	6.82	0.45	6.27	7.59
FL	44	16.05	0.95	14.27	17.75	96	16,87	0,91	14,84	18,94	8	16.27	0.91	15.31	18.00
DL	44	10.60	0.93	8.69	12.40	100	11,73	0,89	9,90	14,50	8	11.17	0.95	9.90	12.75
LIF	44	6.25	0.62	4.67	7.67	97	7,40	0,93	5,76	9,94	8	6.18	0.67	5.32	7.65
BIF	44	2.67	0.34	1.96	3.35	97	2,65	0,30	1,54	3,58	8	2.59	0.35	1.87	2.94
TRL	44	10.86	0.77	9.78	12.57	100	11,75	0,69	9,75	13,15	8	10.88	0.60	9.95	12.03
PL	44	18.47	1.51	15.48	21.90	99	20,35	2,20	10,68	26,10	8	17.84	3.49	10.00	21.83
BPM3	44	11.63	0.64	10.23	12.87	95	11,92	0,68	10,00	13,81	8	11.04	0.69	10.16	12.38
BPP	44	16.04	0.89	14.17	17.66	92	16,90	0,89	15,13	19,65	8	16.29	0.84	15.41	18.20
TBL	44	11.61	0.82	9.41	13.18	94	11,85	0,64	10,42	13,63	8	11.09	0.67	9.55	11.65

bowed; nasals narrow anteriorlyt; zygomatic arches widely expanded and rounded; inferior process of the jugal posteriorly extended to the level of the posterior border of the glenoid fossa; suture between palatines occupied by a triangular to more or less heart-shaped palatal crista; rounded to acute posterior palatal edges, large sphenopalatine vacuities and relatively narrow presphenoids; incisors orthodont to proodont and usually visible from above.

Distribution: *M. australis* is found in Argentina from highland areas (> 2000 m a.s.l.) of Mendoza province in the west and southern Buenos Aires province in the east, south to Santa Cruz province and adjoining parts of southern Chile (Dunnum 2015; Udrizar Sauthier et al. 2016). Populations from high mountain areas of San Juan Province could also correspond to *M. australis*, at least judging by their small size and skull morphology (q.v., Taraborelli et al. 2007).

Taxonomic remarks: No trend in size or morphologic variation was detected throughout the extensive distribution of *M. australis* s.s. We found not evidence indicating that southern Patagonian populations are different, as has been suggested by the taxonomic scheme of Thomas (1921); therefore, no subspecies are recognized.

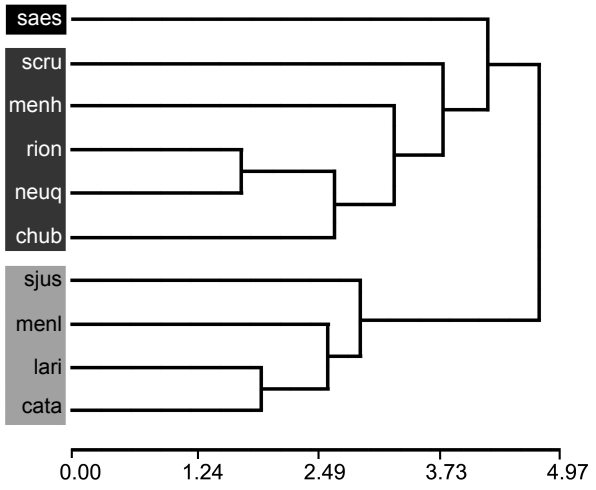

Fig. 9. Dendrogram of unweighted pair-group method of averages of Mahalanobis distances among 10 geographic samples of *Microcavia*. For the acronyms see Materials and Methods.

Microcavia maenas **(Thomas, 1898)**
(Figs. 3-6)

Cavia maenas Thomas, 1898:284.
Caviella australis salinia Thomas, 1921:447 [type locality "Recreo," Catamarca, Argentina].
Caviella australis joannia Thomas, 1921:446 [type locality "Cañada Honda, San Juan. Alt. 500 m," Argentina].

Type locality: "Chilecito, Rioja, 1200 metres," La Rioja, Argentina (Thomas 1898).

Emended morphological diagnosis: A large-size species of *Microcavia* (length of head and body ca. 203 mm, condylo-incisive length ca. 44 mm) having the following combinations of characters: dorsal coloration yellowish gray in some samples (*e.g.*, cata, lari) to brownish in others (*e.g.*, sjun), underparts grayish to yellowish; skull strongly built, wide and larger than in *australis* and the new species described below; dorsal profile of the skull slightly bowed; outer margins of nasals almost parallel-sided; zygomatic arches widely expanded and rounded; jugals posteriorly extended behind the border of the glenoid fossa; long and narrow to long and slightly rhomboidal palatal crista along the suture between palatine bones; usually angled to rounded posterior palatal edge, sometimes with a caudal nasal spine; sphenopalatine vacuities small; presphenoids broad; incisors nearly orthodont and not visible from above.

Distribution: The distribution of *M. maenas* extends up to 2,500 m along montane and hilly areas of Catamarca, La Rioja, Salta, San Juan and Tucumán provinces, and arid lowlands of western Córdoba, north-central Mendoza and northern San Luis provinces. Cabrera (1953) referred an individual trapped in Yavi Chico, Jujuy (MACN-

Table 3. Measurements of the holotypes of some forms associated to *Microcavia*. See Materials and Methods for explanation of the abbreviations

		TLS	CIL	IOC	ZB	BB	NL	DL	TRL	PL	TBL
maenas	BM 96.10.7.12	-	-	11.2	-	-	18.7	12.7	12.1	24.7	-
salinia	BM 21.4.7.6	54.2	50	12.6	32	23.8	18.7	14.5	12.3	26.1	12.9
joannia	BM 21.4.8.5	48.5	45	11.1	28.6	21.9	17.3	12.4	10.3	23.6	11.9
nigriana	BM 11.11.19.3	45.9	43.6	9.4	27.4	22.2	15.6	11.3	11	21.8	12.5

Ma 36.426) to *M. a. maenas*, but our inspection of this specimen led us to re-identify it as *Galea comes*. *Microcavia australis* and *M. maenas* are both present in Mendoza province, although their distributions appears to be allopatric; whereas *M. australis* is restricted to localities at middle and high altitude (> 2000 m a.s.l.), *M. maenas* is found in the lowland terrains east of los Andes (< 1500 m a.s.l.). The distributional ranges of both forms are rather uncertain diffuse and further studies are needed to clarify the limits between them.

Taxonomic remarks: The taxonomic arrangement proposed here, in which *salinia* is recognized as synonym of *maenas*, was suggested earlier by Thomas (1921) who wrote "No doubt [*salinia* is] nearly allied to *C. a. maenas*...". Qualitative and quantitative traits suggest that samples from cata, cord, lari, menc, menl, sjun sjus, salu, salt, and tucu belong to a single lineage for which the oldest available name is *maenas*. Samples from sjus, nearl topotypes of *joannia*, do not differ in size or morphology from other samples referred to *maenas*. Specimens from Salta (salt), were not include in the quantitative analyses because the entire sample was composed by broken skulls; however, the available measurements are close to those of other northwestern samples, warranting its inclusion in *maenas*.

Microcavia jayat **n. sp.**

(Figs. 3-6, 9-10)

LSID: urn:lsid:zoobank.org:pub:7582C06E-83EB-4458-BA58-F19E092ACE67

Microcavia australis salinia: Cabrera, 1953:29; part, not Thomas, 1921.

Microcavia australis salinia: Cabrera, 1961:571; part, not Thomas, 1921.

Microcavia australis: Quintana, 1996:67; part, not Thomas, 1921.

Holotype: An adult female [f] preserved as skin and skull (MACN-MA 17331; figures 9 and 10), and collected on 21 October 1969 by Abel Fornes and Merle L. Kuns (original field number CAF 3070).

Paratype: An adult male [m] preserved as skin and skull (MACN-MA 17333), and collected on 21 October 1969 by A. Fornes and M. Kuns (original field number CAF 3072).

Type locality: Argentina: Santiago del Estero, Pellegrini, Santa Isabel (26°20'S, 64°20'W).

Additional material (localities arranged by increasing latitude): MACN-Ma 17330 [f], MACN-Ma 17332 [f], MACN-Ma 17334 [f], MACN-Ma 17335 [f], MACN-Ma 17336 [f], MACN-Ma 17337 [f], MACN-Ma 17338 [f], MACN-Ma 17339 [f], MACN-Ma 17340 [f], MACN-Ma 17341 [f], MACN-Ma 17342 [f], MACN-Ma 173441 [f], skins and skulls from Santa Isabel, Santiago del Estero; MACN-Ma 36.957, fluid preserved specimen from Cañada de La Costa, Santiago del Estero (27°33'S, 64°52'W); MACN-Ma 28.157 [f], skin and skull from Herrera, Santiago del Estero (28°23'S, 62°20'W); and MACN-Ma 42.96 [f], MACN-Ma 42.97 [f], fluid preserved specimens from Tacañitas, Santiago del Estero (28°37'S, 62°36'W).

Etymology: This species is dedicated to J. Pablo Jayat, a close friend and colleague that in an ongoing productive career is the author of important contributions towards the characterization or the mammal fauna of northern Argentina. The name is a noun in apposition.

Fig. 10. Holotype of *Microcavia jayat* n. sp., from Santa Isabel, Santiago del Estero, Argentina (MACN-Ma 17331): skull in right lateral (above), dorsal (below, left) and ventral (below, right) views, and left dentary (reversed) in labial view. Scale bars = 5 mm.

Measurements of the holotype (in mm): Total length, 195; hindfoot length (with claw), 32; ear length, 18; TLS 45.22; CIL, 41.04; IOC, 10.50; ZB, 27.54; BB, 20.26; NL 13.56; NW, 6.73; FL, 18.00; DL, 11.6; BIF, 2.94; LIF, 5.98; TRL, 10.42; PL, 19.22; BPP, 15.95; BPM3, 11.12; TBL, 11.25. Body mass of the holotype, 60 g.

Diagnosis: A medium-size species of *Microcavia* (length of head and body ca. 187 mm, condiloincisive length ca. 40 mm) having the following unique combination of characters traits: dorsal coloration is yellowish brown, whereas ventral coloration is grayish with patches of pure white hairs on throat, and inner sides of the fore and hindfeet, and the inguinal region; skull strongly built, wide and relatively short; dorsal profile moderately bowed; outer borders of nasals almost parallel-sided; zygomatic arches widely expanded and angled towards its middle portion and with a conspicuous paraorbitary process; jugals posteriorly extended behind the border of the glenoid fossa; suture between palatines occupied by heart-shaped palatal cristae that surpass the posterior border of the palate which is nearly trapezoidal; small sphenopalatine vacuities and relatively broad presphenoids; incisors slightly proodont to orthodont although not visible from above.

Distribution: *Microcavia jayat* is restricted to the thorn-scrub forests of the Dry Chaco ecoregion in the province of Santiago del Estero in north-central Argentina. However, it is likely that the range of *M. jayat* extends to the dry Chacoan forests of the nearby provinces of Salta, Chaco, Cordoba and Santa Fe. Moreover, it is possible, that the specimens referred by Contreras (1966) to *M. a. salinia*, from Tostado, Santa Fe (29°14'S, 61°46'W), for which no vouchers are available, as well as other populations from Santiago del Estero (*e.g.*, Choya; 28°29'S, 64°51'W; see Quintana 1996), are also referable to this species.

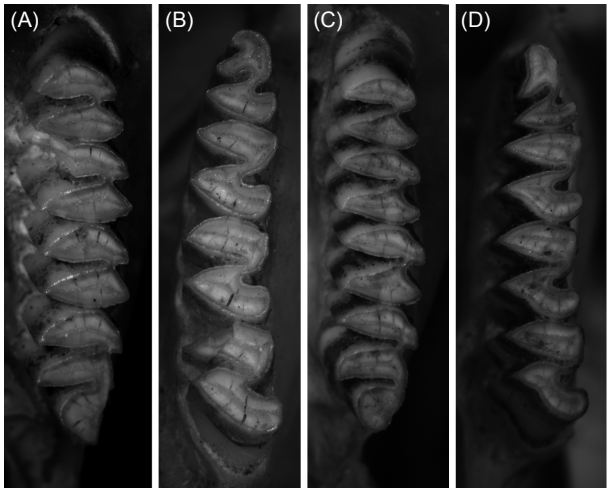

Fig. 11. Left upper and lower left molar rows (A, B) of the holotype (MACN-Ma 17331) and (C, D) paratype (MACN-Ma 17333) of *Microcavia jayat* n. sp., from Santa Isabel, Santiago del Estero, Argentina (MACN-Ma 17331). Scale bars = 5 mm.

Morphological description: *Microcavia jayat* is smaller than *M. maenas* and comparable in size with *M. australis*. Its pelage is fine and slightly hispid; individual hairs are yellowish at the base and brownish at the tip on the dorsum and head and yellowish with two or three brownish bands on the flanks, giving a general yellowish brown appearance, darker and brownish on the midline and head; ears are small and covered by short grayish hairs; a patch of whitish hairs is found behind the ears; eyes are large and are surrounded by a ring of whitish hairs; vibrissae are brownish and fine; manus and pes are covered by yellowish brown hairs; ungual tufts are short on frontclaws and large on hindclaws, but do not surpass the tip of claws; ventral hairs have brownish gray to dark gray bases and whitish distal tips; a “tie” of dark gray hairs is present on the neck; patches of pure white hairs, more or less conspicuous, are present on throat and the internal side of forelegs and sometimes in hindlegs and the inguinal area; palmar and plantar surfaces are dark brownish; plantar surface is squamated, covered by three large, partially fused, interdigital pads and one large thenar pad.

The skull is strongly built, its dorsal profile is moderately bowed; the rostrum is short and relatively narrow; the nasals are slightly vaulted anteriorly, with their outer margins nearly parallel; the naso-frontal suture forms a “V” widely open; the fronto-parietal suture is straight; the interorbital constriction is broad and flat; the orbits are large and rounded; the upper zygomatic process of the maxilla is extended as a plate over the rostrum; the lachrymals are partially interposed between the maxilla and premaxilla; the masseteric fossa of the zygomatic arch is deep and well defined; a conspicuous paraorbitary process is present; the jugal is posteriorly extended beyond the border of the glenoid fossa; the posterior process of the squamosal is straight; the posterior margin of the upper diastema is not vertical; the incisive foramina are nearly triangular in outline, with rounded margins in its posterior border; the palate is concave, with the palatine bones occupying the posterior half of the palate; the suture between

palatines is occupied by heart-shaped palatal cristae that surpass the posterior border of the palate; the posterior margin of the palate is nearly trapezoidal in outline; the parapterygoids are large; the roof of the mesopterygoid fossa is well ossified, with small sphenopalatine vacuities along the presphenoid; the limit between the mastoid and paraoccipital process is at the same level of the auditory meatus; the occipital condyles are ovate and large and positioned above the ventral surface of the auditory bullae; the tympanic bullae are voluminous, with its external auditory meatus relatively short; the paraoccipital apophyses are short.

The mandible is low and slender; in labial view, the notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle lies between the p4 and m1; this notch is continued by a horizontal crest that extends anteriorly to the level of the anterior lobe of m1; the dorsal fossa of the horizontal crest is deep; the lateral crest originates at the level of the m1 and is horizontal; the coronoid process is small and triangular and is oriented backwards; the condyloid process is level with or slightly higher than the coronoid.

The upper incisors are orthodont to proodont, with white enamel; the upper toothrows are anteriorly convergent, with the P4s almost in contact by its medial side; the P4 and M1-M2 are constituted by two lanceolated prisms of dentine, surrounded by a continuous wall of enamel and linked by small enamel isthmus; the lingual apex of each prism is slightly turned backwards; those lobes of the P4 are narrow than those on M1-M2 which are subequal in size; the hipoflexus on M1-M3 is long, with its borders nearly parallel along most of the teeth and slightly divergent to the lingual portion; the primary external flexus on M1-M3 is short and wide; the M3 has a rounded to drop-shaped enlargement, attached to the second prism; the p4 is smaller than m1-m3 both anteroposteriorly and transversely. The anterior lobe of p4 is obliquely oriented and heart-shaped, with a well developed anterior projection; the posterior lobe is more narrow and shorter than the posterior lobe of the molars; the anterior lobe on m1-m3 is more lanceolate than the posterior lobe; hypoflexid on m1-3 is funnel-shaped and wide, with a rounded lingual apex; primary internal flexids are wide and slightly oriented posteriorly.

Variation: Ventral coloration is variable among individuals, with a gradient from dark gray to whitish. At least two individuals (MACN-Ma 28.157, MACN-Ma 17340) have a markedly brownish dorsal coloration, as is usually seen in *M. australis*. White patches on throat, internal side of the fore and hindfeet and inguinal region are very conspicuous in some specimens (*e.g.*, MACN-Ma 17332, 17334, 17338), but weakly expressed in others.

Morphological comparisons: Morphological differences between *M. jayat* n. sp. and *M. australis* and *M. maenas* were discussed under the results section. In *M. niata* the skull is strongly bowed, with a very short and high rostrum (upper diastema length < upper toothrow length), and has a curved posterior process of the squamosal. *M. shiptoni* has proportionally smaller tympanic bullae, with proportionally larger external auditory meatus and the additional prism in the upper third molar is smaller. Both in *M. niata* and *M. shiptoni* the upper incisors are proodont and visible from above. *M. jayat* n. sp. differs from the fossil species *M. chapadmalensis*, *M. criollensis*, *M. reigi*, and *M. robusta* by its much smaller size (length of tootrow ca.11 mm vs. 12-18 mm in fossil species; q.v., Ubilla et al. 1999) and less robust cranium.

Natural History: We know very little about the natural history of this species. The specimens referred to *M. jayat* were collected in the Dry Chaco ecoregion. The Dry Chaco is characterized by thorn scrub xerophytic forest vegetation dominated by *Aspidospermum quebracho-blanco* and *Schinopsis quebracho* with a subcanopy made up of several species of Fabaceae and arboreal cacti. Wooded areas are intermixed with open savannas, mostly dominated by grasses, shrubs, and trees. The weather is subtropical, strongly seasonal, with a dry season during winter months and high temperatures during the entire year; the mean annual temperature is 21.5°C, with maxima reaching 50°C; precipitation are in the order of 700 mm per year (The Nature Conservancy 2005).

Conservation: Given the current knowledge, this species could be listed as Data Deficient, since it is only known from < 10 localities and most of the aspects of its natural history are unknown. The Dry Chaco has been under severe perturbation due to logging and livestock grazing and during recent agricultural expansion (mostly due to increased soybean crops; Vallejos et al. 2015). For example, deforestation in Argentinean Dry Chaco amounted to an average of 100,000 hectares per year between 2001 and 2007. As a corollary of all of these activities, the Dry Chaco faces severe problems of desertification and erosion of its soils (The Nature Conservancy 2005).

DISCUSSION

Delimiting species is a challenging task and choosing an appropriate criterion is the subject of ongoing discussion (de Queiroz 1998; Camargo and Sites 2013). Recent studies aimed at determining species boundaries on mammals have relied heavily on the analyses of molecular markers (*e.g.*, Dunnum and Salazar Bravo 2010a; D'Elía et al. 2015) or via integration of different sets of evidence (*e.g.*, Lanzone et al. 2007; Phuong et al. 2014; Hanson et al. 2015; Jayat et al. 2016; Balakirev et al. 2017; Guerrero et al. 2017). However, in the absence of molecular data, the use of morphological characters, both qualitatively and quantitatively analyzed and retrieved from large series of specimens, remains as a common procedure for delimiting species (*e.g.*, Gaubert and Antunes 2005; Pacheco et al. 2014; Woodman and Timm 2016). The reasoning behind this practice could be posed as follows: i) there is, in general, less morphological variability within species than among them, ii) qualitative and quantitative morphological discontinuities are usually the result of population isolation, and iii) given that morphology is, at least partially, genetically encoded, the existence of morphological discontinuities implies distinct genetic pools and as such, the existence of independent lineages. Here we followed this reasoning that searching for morphological diagnosability, a pivotal point in several species concepts (see the discussion in do Prado and Percequillo 2017).

Our quantitative and qualitative analyses of a large sample from geographically distant populations of *Microcavia australis* supports that this taxon, as currently understood, encompasses a complex of three distinct species. Each of these is diagnosable by a unique combination of character states. To accommodate our hypothesis of species level lineages within *australis* s.l., we remove from the synonymy of *australis* the nominal form *maenas* and apply it to montane populations of north-central Argentina and nominate a new taxon for a lineage endemic to the Dry Chaco. The absence of polymorphism in some character states, such as the presence of paraorbitary process, the form of the anterior border of the mesopterygoid fossa and the size and shape of the sphenopalatine vacuities are indicative of the absence of gene flow between *M. jayat*, the species described here, and the other species of the genus (cf. Wiens and Severdio 2000).

The taxonomy of Caviidae was the subject of recent contributions, including molecular (*e.g.*, Dunnum and Salazar-Bravo 2010a, 2010b) and morphological (*e.g.*, Bezerra 2008) studies. These works recognized that the diversity within the genera *Cavia* and *Galea* was underestimated. For example, Dunnum and Salazar-Bravo (2010a) identified candidate species of *Galea*, referring two of them with the available names *comes* and *leucoblephara*, and leaving one unnamed. Although no similar studies are available for *M. australis*, the geographically circumscribed study of Sassi et al. (2011b), suggested that this taxa is a species complex. In addition, distinctions between lowland populations of *M. maenas* and highland populations of *M. australis* from west-central Argentina are also supported by significant variations in the morphology and physiology of the digestive tract (Sassi et al. 2007, 2010), foraging preferences (Sassi et al. 2011a), size of social groups, agonistic behavior (Taraborelli 2009; Taraborelli and Moreno 2009), and antipredatory responses (Taraborelli et al. 2009).

Caviids constitute a diverse clade of caviomorph rodents, distributed across the major South American biomes, particularly in drylands where they reach their highest species richness (Ojeda et al. 2016). The description of the new species of *Microcavia* is noteworthy, since these animals are relatively abundant, conspicuous, and diurnal-crepuscular inhabitants of open shrublands and grassland environments. However, the Dry Chaco ecoregion is an area poorly known from a mammalogical perspective (Teta et al. 2016 and references therein; see also Jayat et al. 2016), thus, the finding of a new species from this ecoregion is not totally unexpected. Additional data, especially from molecular markers, is much needed to test the taxonomic hypotheses presented here, as well as to assess the phylogenetic relationships among the species of *Microcavia*. As *Microcavia* has a large distribution, occurring on the Andes and lowlands, it represents a good model to assess the role of the Andean orogeny and the development of arid and semiarid lowland habitats in mammalian diversification.

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Authors' contributions: PT, RAO, SOL and GD designed the study and wrote the manuscript. PT performed the statistical analyses. PT and RAO analyzed and measured the specimens. All authors participated in revising the manuscript. All authors read and approved the final manuscript.

Competing interests: Authors declare that they have no conflict of interest.

Availability of data and materials: Key datasets of the manuscript are presented as supplementary files.

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Ethics approval consent to participate: Not applicable.

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Supplementary 1 - **Appendix.** List of the specimens of *Microcavia* examined in this study and their collecting localities in Argentina. Localities are grouped by provinces and departments. Studied specimens are housed at the following mammal collections: BM, The Natural History Museum (London, UK); CEM, Colección Elio Massoia (acquired by the Fundación de Histora Natural Félix de Azara, Ciudad Autónoma de Buenos Aires, Argentina); CMI, Colección de Mamíferos del Instituto Argentino de Investigaciones de Zonas Áridas (Mendoza, Argentina); CML, Colección de Mamíferos de la Facultad de Ciencias Naturales e Istituto Miguel Lillo (San Miguel de Tucumán, Argentina); CNP, Colección de Mamíferos del Centro Nacional Patagónico (Puerto Madryn, Argentina); MACN, Colección Nacional de Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Ciudad Autónoma de Buenos Aires, Argentina). (download)

Supplementary 2 - Fig. 1sm. Dorsal and ventral views of the skins of *M. australis* (A, D; MACN-Ma 49.115), *M. maenas* (B, E; MACN-Ma 34.58) and *Microcavia* n. sp. (C, F; MACN-Ma 17331). (download)

Supplementary 3 - Table 1s. Classification matrix determined by the discriminant function. See matherials and metods for abreviations. (download)

Supplementary 4 - Table 2s. External measurements for individual specimens of *Microcavia.* (download)